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A SPATIALLY EXPLICIT STOCHASTIC MODEL DEMONSTRATES THE FEASIBILITY OF WRIGHT'S SHIFTING BALANCE THEORY

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Abstract.—Recently there has been a resurgence of theoretical papers exploring Wright's Shifting Balance Theory (SBT) of evolution. The SBT explains how traits which must pass through an adaptive valley may evolve in substructured populations. It has been suggested that Phase III of the SBT (the spread of new advantageous traits through the populations) proceeds only under a very restricted set of conditions. We show that Phase III can proceed under a much broader set of conditions in models that properly incorporate a key feature of Wright's theory: local, random migration of discrete individuals.

Key words.—Diffusion approximation, Sewall Wright, shifting-balance theory, stochastic simulation models, substructured populations.

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Coyne et al. (1997) recently sounded the death knell of Wright's shifting balance theory of evolution (SBT). While they acknowledge that "Given the multifarious nature of evolution, almost every conceivable scenario must occasionally occur," they report to have found "no compelling evidence that Wright's shifting balance theory accounts for the evolution of a single adaptation, much less a significant proportion of adaptations, in nature. Until such evidence is at hand," they continue, "we favor the view that adaptations are usually produced by Fisherian mass selection, a process that is not only more parsimonious than the SBT but has also been shown to occur widely (Endler 1986)." Following Haldane (1959), they conclude that the third phase is the weakest link in the Shifting Balance Theory. (In the third phase an advantageous trait that evolved in one of the subpopulations in Phase I and became fixed in that subpopulation in Phase II, spreads throughout the region of subpopulations.) Coyne et al. (1997) use several theoretical models to argue that the third phase proceeds only under a restrictive set of conditions, and they infer that those conditions will be rare enough in nature so that the third phase need not be considered a major force in evolutionary change. The models they consider include both deterministic (Crow et al. 1990; Gavrilets 1996) and stochastic models (Lande 1985; Barton and Rouhani 1987, 1993; Rouhani and Barton 1987). We argue, however, that these models have not yet explored the third phase of the SBT properly and that it is yet too early to dismiss Wright's theory.

When one looks at the models that have been used to study Wright's third phase, two things are apparent: many of them are deterministic and most of the stochastic models are island models which assume nonlocal movement (Table 1). In addition, all of the models have assumed that migration is a deterministic process (i.e., there is a tacit assumption of infinite population size during the migration phase).

For example, Barton and Rouhani (1993) use a diffusion model to demonstrate that the third phase of the shifting balance occurs when selection, migration, and drift are of the

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TABLE 1. Most models for Phase III of the shifting balance have not involved stochastic and locally spatially explicit dynamics. It is in the upper left hand corner that Wright envisioned the third phase to most readily proceed and most of the models have ignored this region. "Island" models ignore the actual arrangement of local demes in space, while "stepping stone" models are spatially explicit at the demic level and limit migration to the most nearby populations. Previous stepping stone models of Phase III have all been deterministic (lower left corner), whereas the stochastic island models (upper right corner) have only included random allelic drift within populations but omit the allelic drift resulting from random sampling of migrants from a finite population.

	Assumptions about migration	
	Stepping stone	Island
Stochastic	this paper	Allelic drift within local demes, deterministic migration e.g., Lande 1985; Barton and Rouhani 1993; Rouhani and Barton 1993
Deterministic	e.g., Wade and McCauley 1988; Crow et al. 1990 (two demes); Phillips 1993 (two demes); Gavrilets 1996 (multiple demes)	e.g., Slatkin 1977; Wade and McCauley 1988

same order. However, their model uses infinite population size during the migration phase, and because it is an island model, the influence of local migration is lost. This is very different from the process of drift and local spread that Wright envisioned for the third phase of the SBT (Wright 1988; Turner 1992).

Gavrilets (1996) used a small, coupled-map lattice to conclude that in two dimensions the third phase proceeds under a very restricted set of conditions. The model, however, does not have stochastic effects (on allelic frequency) in either the migration or selection components. Moreover, Gavrilets's (1996) conclusions are based on the model's behavior for very weak selection only (as opposed to what is often found in wild populations [Endler 1986]).

A hint that Phase III may proceed more readily than Coyne et al. (1997) conclude comes from the work of Durrett and Levin (1993). "Case 2" of Durrett and Levin (1993) mirrors the third phase of the shifting balance wherein competition between "hawks" and "doves" is analogous to disruptive selection at a single locus in a diallelic genetic system. When the process was modeled with a nonspatial dynamical system, it showed two stable equilibria at all "hawks" and at all "doves," and an unstable saddle point. Depending on initial conditions, one peak or the other was reached, much like what has been seen in the models reviewed in Coyne et al. (1997). However, when a discrete spatial model with stochastic local migration was used, fixation of the dominant type (analogous to phase III of the SBT) always occurred. The system converged to fixation of the same dominant type for generic initial conditions.

To follow up this hint, we constructed and simulated an analogous two-dimensional stepping-stone genetic model (Appendix 1). Like other models (e.g., Gavrilets 1996), this model ignores adaptive topographies generated by epistatic interactions. However, it captures the essence of Wright's SBT, including nonadditive genetic variance, and an adaptive topography that has two local maxima separated by an adaptive valley. The model has (integer) finite population size, incorporates within-deme drift, and uses stochastic local migration. We found that phase III proceeds over a much wider set of parameter values than previously noted. Barton and Rouhani (1993) predict that Phase III should be favored when $0.1 < Nm < 1$ and should proceed more quickly when $0.01 < Ns < 10$ (N = number of individuals per deme, s = selection coefficient, m = migration probability). In the simulation model, Phase III proceeds in all seven replicates when $Nm = 0.05$, albeit very slowly (Table 2a). We found that for $Nm = 5$, $Ns = 25$ when $N = 50$; and for $Nm = 10$, $Ns = 50$ when $N = 100$ (Table 2a), Phase III proceeds rapidly for all replicate runs of the model, which is unexpected given Barton and Rouhani's (1993) results. Figure 1a demonstrates the time course of one replicate of the simulation model where Phase III proceeds.

For the parameter values of selection = 0.05 and migration = 0.01, Gavrilets (1996) predicts that a polymorphism should be maintained. In almost every replicate of the simulation model the more fit peak is reached for low N ($N = 50$ and $N = 100$), but not for larger N ($N = 500$ and $N = 1000$). Even when values of selection and migration are well within the range for which Gavrilets (1996) predicts the less fit peak

TABLE 2. Median (1st and 3rd quartile) time until fixation of the more fit "A" allele in the simulation model of the shifting balance theory. The range of values for the parameters is s = (0.0005, 0.005, 0.05, 0.5), m = (0.001, 0.003, 0.01, 0.03, 0.1), and n = (50, 100, 500, 1000). The maximum time was 30,000 generations. Each parameter combination was replicated seven times. Entries with a median time to fixation equals 30,000 indicate that the proportion of demes with an allelic frequency of > 0.5 was greater than 50%, suggesting that the system was on its way to fixing the A allele in all the demes in those replications, but had not yet achieved it.

s	m	n	Time to fixation	Number reps Phase II (Max 7)
(a) Constant deme size				
0.0005	0.001	50	30000 (30000, 30000)	1
0.005	0.001	50	30000 (30000, 30000)	1
0.05	0.001	50	22662 (18208, 27928)	7
0.05	0.003	50	7421 (6922, 8387)	7
0.05	0.01	50	2196 (2050, 2429)	5
0.5	0.03	50	28036 (25501, 30000)	5
0.5	0.1	50	201 (184, 221)	7
0.005	0.001	100	20390 (19493, 23388)	3
0.05	0.001	100	30000 (30000, 30000)	1
0.005	0.003	100	11888 (11888, 11888)	1
0.05	0.003	100	19044 (15772, 23400)	7
0.05	0.01	100	3863 (2984, 4401)	7
0.0005	0.1	100	21698 (19366, 24030)	2
0.5	0.1	100	383 (368, 494)	7
0.005	0.001	500	26655 (24484, 28507)	5
(b) Varying deme size				
0.5	0.001	50	7754 (6413, 8349)	5
0.5	0.003	50	2276 (1936, 2733)	6
0.5	0.01	50	807 (743, 853)	5
0.5	0.03	50	456 (441, 473)	4
0.5	0.1	50	114 (114, 114)	1
0.05	0.001	100	8678 (8678, 8678)	1
0.5	0.001	100	7014 (5606, 9554)	5
0.0005	0.003	100	30000 (30000, 30000)	1
0.05	0.003	100	1917 (1767, 1929)	3
0.5	0.003	100	2415 (2368, 2482)	4
0.0005	0.01	100	30000 (30000, 30000)	1
0.005	0.01	100	19201 (18610, 19791)	2
0.5	0.01	100	1123 (986, 1226)	3
0.0005	0.03	100	13005 (13005, 13005)	1
0.5	0.03	100	366 (351, 391)	3
0.5	0.1	100	127 (127, 127)	1
0.0005	0.001	500	30000 (30000, 30000)	6
0.005	0.001	500	6558 (5196, 6739)	5
0.05	0.001	500	4131 (3852, 5134)	6
0.5	0.001	500	7375 (7142, 7778)	3
0.0005	0.003	500	30000 (30000, 30000)	7
0.005	0.005	500	3771 (3648, 4203)	7
0.00	0.003	500	2650 (2523, 2886)	4
0.5	0.003	500	3776 (3056, 3691)	3
0.0005	0.01	500	13176 (11883, 19404)	7
0.005	0.01	500	11507 (10665, 20217)	5
0.05	0.01	500	1164 (1164, 1164)	1
0.5	0.01	500	1549 (1426, 1668)	4
0.5	0.03	500	498 (579, 520)	3
0.5	0.1	500	125 (125, 125)	1
0.0005	0.001	1000	30000 (30000, 30000)	7
0.005	0.001	1000	5474 (4826, 5675)	5
0.05	0.001	1000	4975 (4501, 6051)	6
0.5	0.001	1000	11165 (10466, 13680)	5
0.0005	0.003	1000	20459 (19248, 20627)	7
0.005	0.003	1000	6605 (6214, 8489)	6
0.05	0.003	1000	3938 (3756, 4120)	2
0.5	0.003	1000	3195 (2701, 3308)	5
0.0005	0.01	1000	15688 (13220, 20347)	7
0.5	0.01	1000	1476 (1346, 1764)	6
0.5	0.03	1000	463 (417, 514)	5

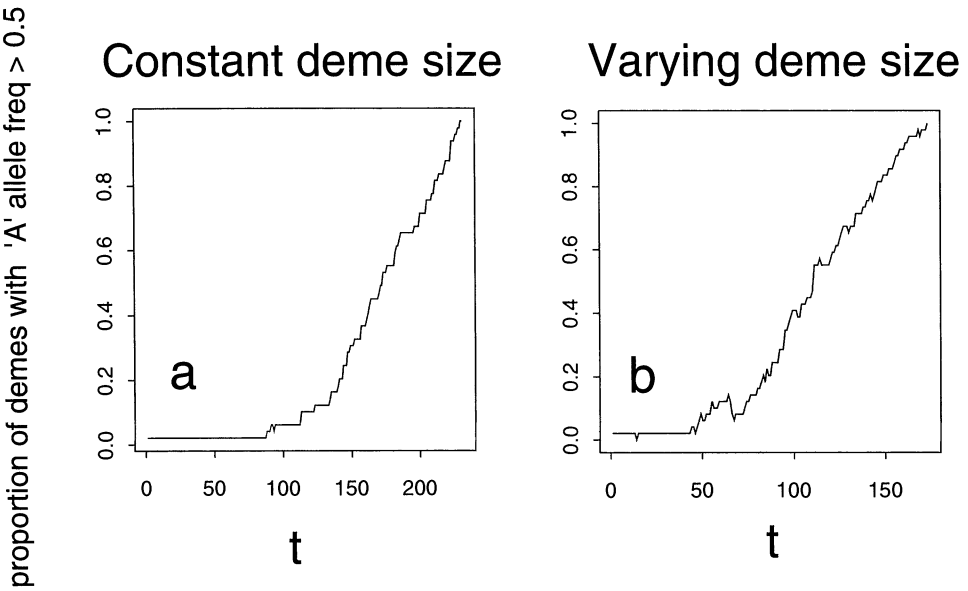

FIG. 1. The dynamics of the simulation model in one of the replicates in which the more fit peak was reached for parameter values where Barton and Rouhani (1993) predict that the third phase of shifting balance should not be favored. Plot (a) shows the dynamics when the population size, N is fixed. In (b) the size of each deme varied randomly and independently between generations, with a uniform distribution on (0, $2N$) and hence mean deme size N. Plots give the proportion of demes in which the more fit allele has reached a frequency of $> 50\%$. Note the changes in the x- and y-axes among the plots.

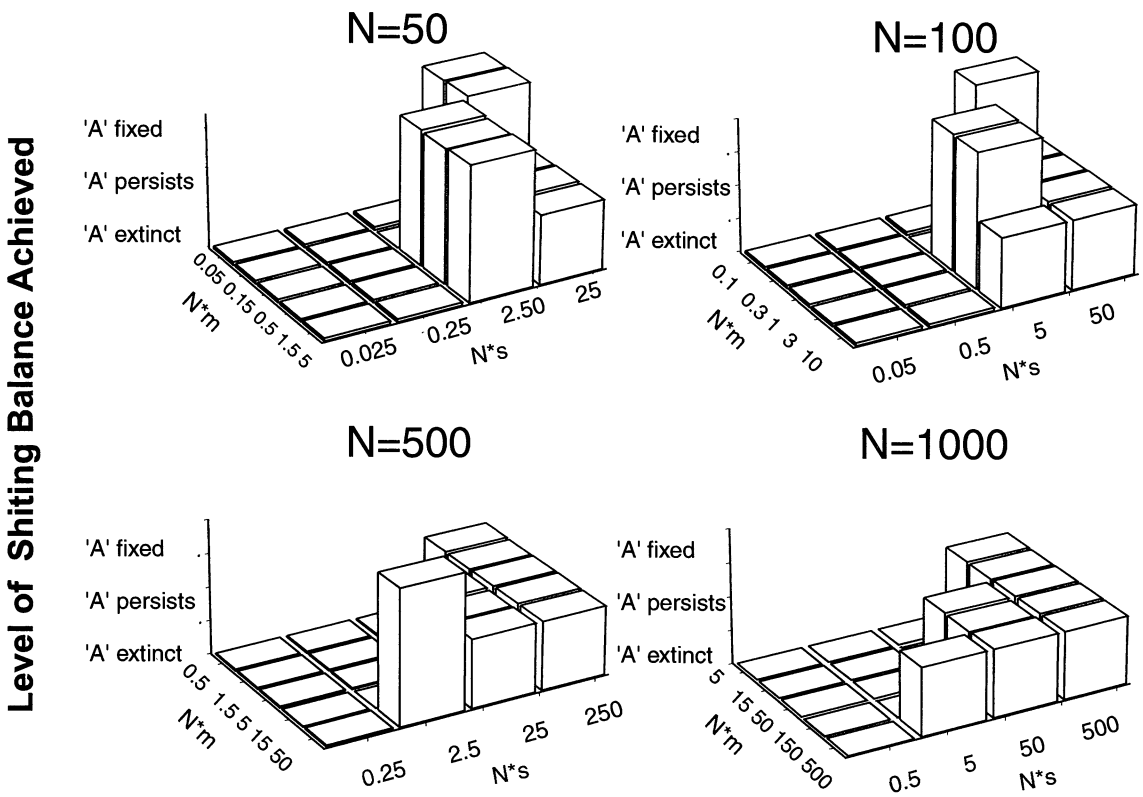

FIG. 2. In each of the four plots, the z-axes represent three possible states of the model run: near the origin, the less fit a allele becomes fixed in the population; midway up the z-axis the A allele persists in the deme where it originally started, but never spreads throughout the region; and at the top of the z-axis the more fit A allele spreads and is fixed in the region. Each plot represents a different value of N.

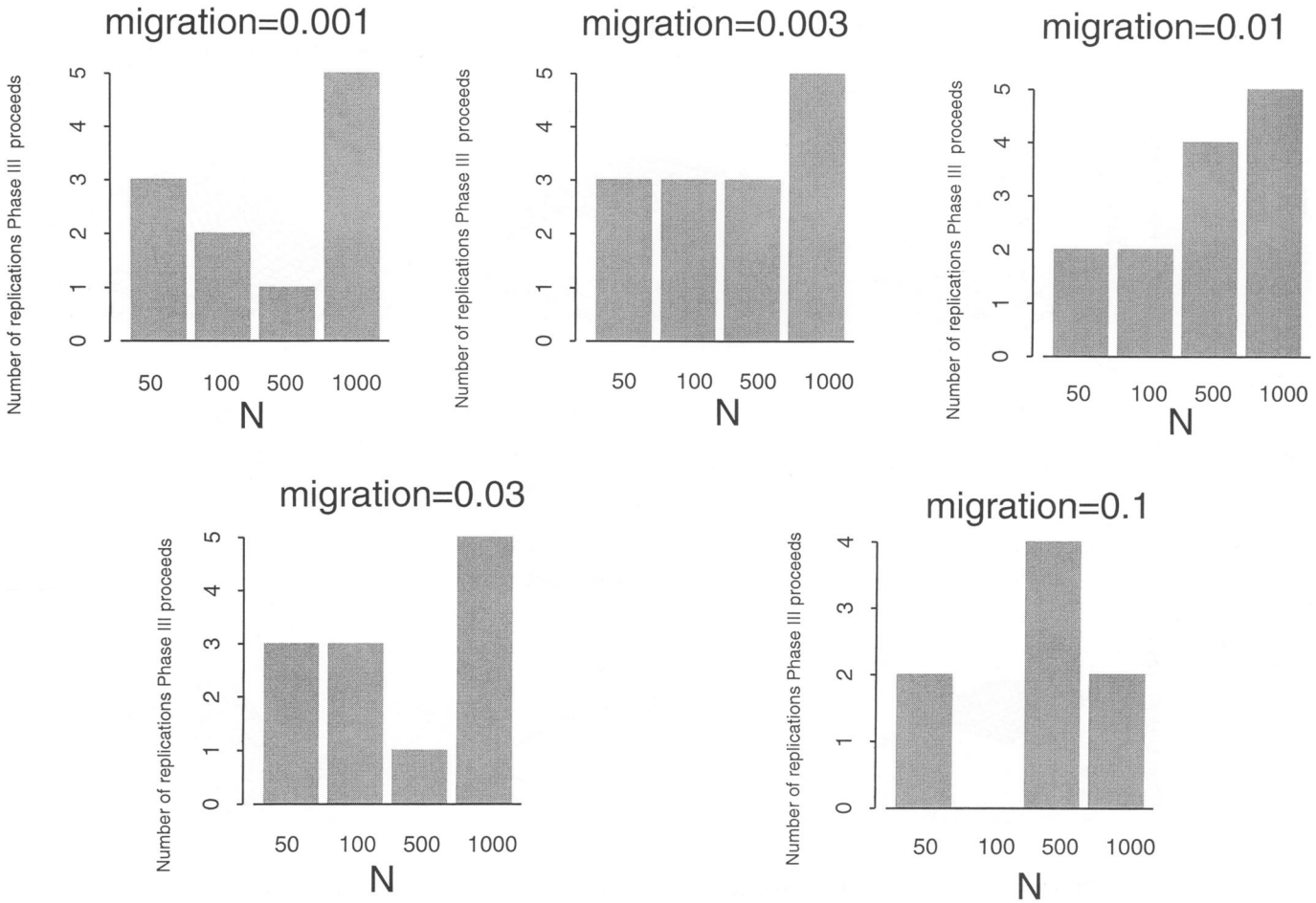

FIG. 3. Shows the overall frequency of the more fit allele in the region as a function of migration, selection, and randomly varying deme size as described in Figure 1 legend. Here $s = 0.5$ (the maximum selection value found in the wild [Endler 1986]). In this range the allele which becomes fixed seems to vary unpredictably, following no simple rules for differing values of migration and population size.

should be maintained ($P = 0.33$, $m/2s = 0.33$), in three of 15 replicates of the simulation model at N = 100 Phase III proceeded.

Figure 2 plots where Phase III proceeded, over the range of parameter values explored in the simulation model at different values of N (deme size). Table 2a presents a much different structure than that predicted by Barton and Rouhani (1993) and Gavrilets (1996). These two examples show that stochastic, local migration can greatly expand the range of conditions under which Phase III can proceed. Moreover, if we allow random fluctuations in population size, such as might be caused by environmental stochasticity, the results change even more dramatically. Table 2b shows that with a variable population size, the range of parameter values for which Phase III proceeds, is dramatically expanded over what is expected given prevailing theory. For example, in Figure 3 nearly half the replicates showed a peak shift regardless of population size or migration rate. Whether or not the peak shift occurs seems to be dominated by chance events within the model and is not strongly affected by the parameters typically implicated in controlling the third phase. Figure 1b indicates that Phase III can proceed more rapidly when assisted by random fluctuations in deme size.

The potential significance of drift in allelic frequencies due to local random migration is evident even in a simple two-deme model, which can be analyzed via a standard diffusion approximation (Appendix 2). In this model the allelic fitnesses cover the same range as those in the simulation model. Here we consider a single peak shift in deme 2, which starts at a low frequency p of the more fit allele A, while neighboring deme 1 has already become fixed for the more fit allele. This should approximate the situation if the fitness advantage of the A allele is large enough that reverse shifts are essentially impossible. Each generation, after random mating, each individual in deme 1 has probability m of migrating to deme 2 (i.e., the number of migrants is binomial), and an equal number of migrants leaves deme 1 to maintain constant deme size. As in the full model, mating and selection within demes are stochastic with discrete individuals.

In the diffusion approximation, stochastic migration always led to a more rapid shift to the more fit peak, and this effect increased with increasing levels of migration (Fig. 4). Allelic drift resulting from local stochastic migration has been largely ignored, with migration typically modeled deterministically as mN. However, our simple diffusion model for peak shifts in a single deme shows that deterministic

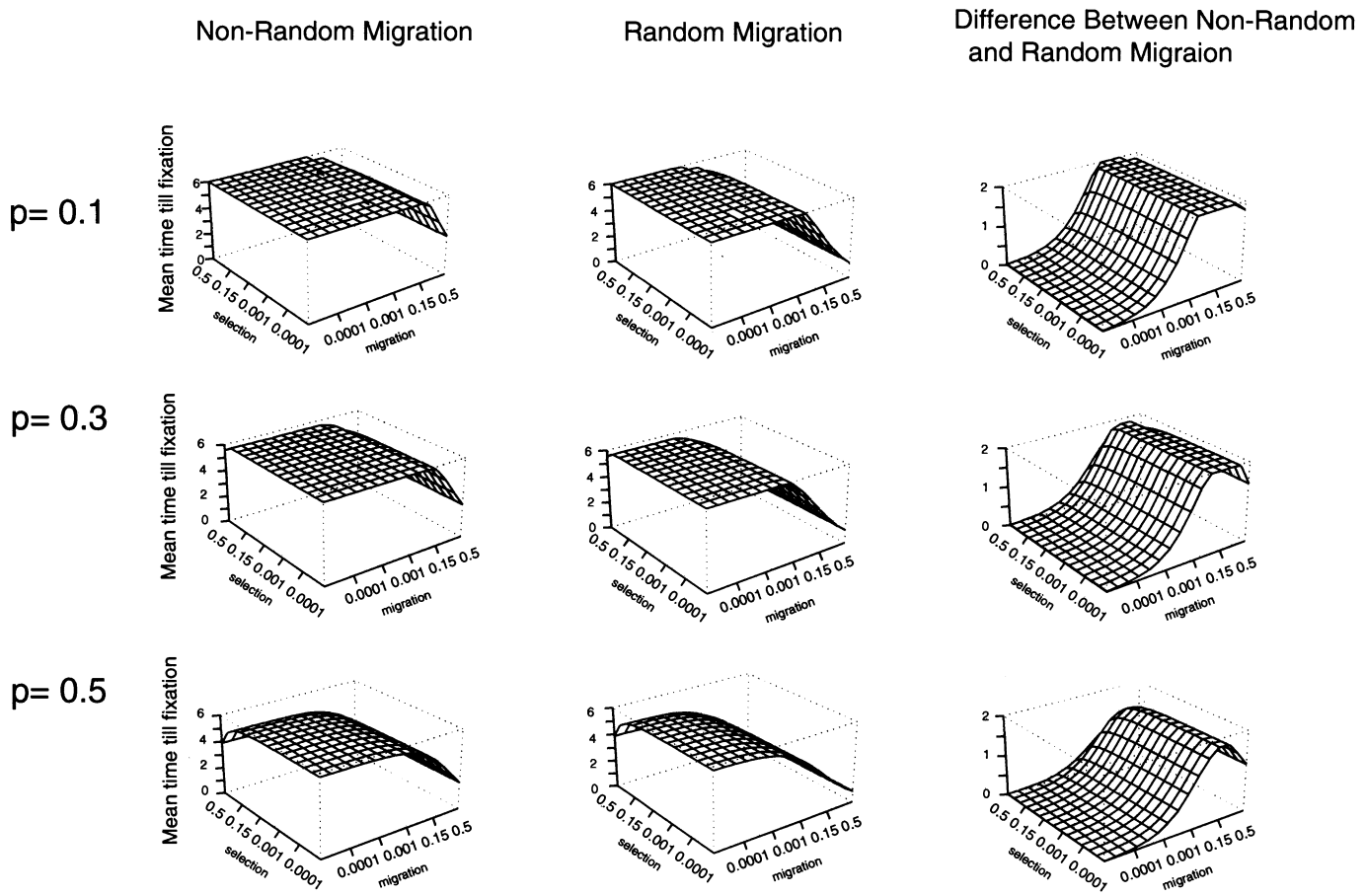

FIG. 4. Results from Diffusion model. Each of plots graphs $t_f/2N$ as a function of selection and migration, where t_f is the expected time until fixation. The rows are for different starting values of p (0.1, 0.2, 0.3) and the columns are for nonrandom migration, random migration, and the difference between the two cases. Note that for every value of s and m in the model, random migration always decreases the time to fixation of the more fit allele, suggesting that the shifting balance may proceed more readily when migration is random.

modeling of migration omits a potentially important factor in local peak shifts and hence in phase III of the SBT.

Is it time to set aside the shifting balance theory? We argue that it is premature to dismiss the SBT until models have been explored that match more closely what Wright originally envisioned (Levin et al. 1997) including all three phases of the SBT. The SBT is certainly more complex than Fisherian mass selection, but the interaction of genetics, ecology, population structure, metapopulation dynamics, and stochasticity are all part of nature's reality and can influence the tempo and mode of evolution.

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APPENDIX 1

The model presented here is a stepping stone model on a square grid in which a diallelic diploid population (alleles *A* and *a*) inhabits each local deme. The state variables for the models are the (integer) number of individuals of each genotype in each local deme. The fitnesses (relative survival probabilities of offspring) for the three genotypes *AA*, *Aa* and *aa* are $1 + k$, $1 - s$ and *1* respectively. In all cases, $k = s/(1 - s)$ so that $1 + k = 1/(1 - s)$. Changes in genotype frequencies due to mating, selection and migration were all modeled as stochastic "coin tosses" (that is, as draws from the appropriate trinomial distributions determined by the current genotype frequencies, migration rate, deme size, and fitnesses). Migration is symmetric and limited to adjacent grid cells, and selection is soft (i.e., the total number of individuals per deme is not affected by the allele frequencies). Mating was random within demes, so that the offspring genotypes prior to selection were chosen in Hardy-Weinberg proportions. The model was run on a 7 x 7 grid of demes with the center deme initialized as fixed at the higher-fitness peak (all *AA*), and all others fixed at the lower-fitness peak (all *aa*). Results are reported for simulations of length 30,000 generations.

APPENDIX 2

For the two-deme model with one-way migration, the frequency of the A allele in the second deme after one round of selection, random mating, and migration is given by $p_2 = p1 - pm + m$, where

$$P_1 = \frac{p^2(1 + k) + p(1 - p)(1 - s)}{p^2(1 + k) + 2p(1 - p)(1 - s) + (1 - p)^2}$$

p is the initial frequency in the second deme, $p_1 \sim 1/(2N)\ \mathrm{B}(2N,P_1)$ and $m \sim 1/(2N)\mathrm{B}(2N,\boldsymbol{m})$ if migration is stochastic, otherwise m equals the mean migration rate $\boldsymbol{m}$. The parameters s and k are defined in the legend to Figure 4. Note that if m is constant, our model is formally equivalent to a model of selection and one-way mutation to the more favorable allele. The diffusion approximation for the model can be derived from the expression above for p_2 by standard methods (e.g., Karlin and Taylor 1981). The infinitesimal mean and variance for the diffusion approximation are given by $\mu(p) = p(p(\kappa + 3\zeta) - p^2(\kappa + 2\zeta) - \zeta - \eta) + \eta$, $\sigma^2(p) = \eta + p(1 - p)$, respectively where

$$s = \zeta/2N,\ k = \kappa/2N,\ m = \eta/2N.$$

Mean time to fixation of the favorable allele in the diffusion approximation is then computed directly from the infinitesimal moments; for the formulas see Ewens (1979).

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NEGATIVE MATERNAL EFFECT REVISITED: A TEST ON TWO POPULATIONS OF *ORCHESELLA CINCTA* L. (COLLEMBOLA: ENTOMOBRYIDAE)

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Abstract.—A Dutch population of *Orchesella cincta* had been demonstrated to exhibit a negative maternal effect on age at first reproduction, which caused alternation of short and long generations. The adaptive significance of such a mechanism was assumed to be associated with the bivoltine life cycle of Dutch *O. cincta*. We expected that it would be absent in a non bivoltine population sampled in Siena, Italy. To test this hypothesis we performed a parent-offspring regression experiment with both populations simultaneously. The experiment showed that there was no negative maternal effect in both populations. We leave open the question of the cause of the discrepancy between the previous result with the Dutch population and the present result. The results of our experiment were also used to determine heritabilities of the traits age, mass and number of molts at first reproduction, and size of the first clutch. The estimates of heritabilities were often not significantly different from zero, especially in the Italian population which had only one significant heritability.

Key words.—Heritability, maternal effect, *Orchesella cincta*, reaction norm.

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Phenotypic plasticity is the environmental part of phenotypic variation, and the function that describes, for a certain genotype, the dependence between a phenotypic value and an environmental variable is called the norm of reaction (Stearns and Koella 1986; Roff 1992; Stearns 1992). From an evolutionary point of view it is expected that an organism will respond to all environmental variation that it is likely to meet during its lifetime in such a manner that fitness is maximized. There are many ways in which environments vary, all of which can be characterized by the categories